CONCLUSIONS

LITERATURE CITED

Some Effects of Mycorrhizae on the Phosphorus Nutrition of Monterey Pine Seedlings[1]

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THE role of mycorrhizae in the growth of coniferous trees is of interest not only as an uncommon ecological relationship and a matter of concern in afforestation but also as a problem to be solved before the mineral nutrition of such species can be satisfactorily related to the chemical properties of soils. The marked effects of mycorrhizal inoculation on the growth of coniferous seedlings are well known (3, 7, 10, 12)[3] but the mechanism of mycorrhizal benefit is still obscure. The investigations of McComb (6, 7), in particular, have singled out phosphorus nutrition as a probable major factor in the response of coniferous seedlings to mycorrhizal infection on certain soils. The experiments reported here were designed to test the effect of mycorrhizae on the phosphorus nutrition of Monterey pine, *Pinus radiata*, D., Don., seedlings under various conditions.

PROCEDURE

General Methods

For Experiment 1 a synthetic soil was prepared from quartz sand, bentonite, and difficultly available phosphatic minerals. Two prairie soils, an O'Neill sandy loam from near Ames, Iowa, and a Carrington silt loam from near Token Creek, Wis., were used for Experiments 2 and 3. Previous studies of mycorrhizal response and analytical data concerning these latter soils have been reported by McComb (78), and White (16) and Rosendahl[4] (12), respectively. The test crop in each case was Monterey pine. In Experiments 1 and 2 sterile germinating seeds of known weight classes were sown whereas 10-week old seedlings, grown in 1/10 Hoagland's nutrient solution, were used for Experiment 3. *Boletus luteus*, grown on wheat, was introduced as the inoculating fungus in most cases but, as noted, no certain success was obtained. In all cases where inoculum was added the noninoculated treatments received an equal amount of sterile substrate.

The culture vessels in Experiments 1 and 2 were No. 1 cannery tins which held 575 grams of the synthetic soil, 454 grams of Carrington soil, or 500 grams of the O'Neill soil. Glass cylinders of about 200 ml volume were used in Experiment 3. Since the plants were grown in the greenhouse the vessels were placed in trays of water during the summer to reduce soil temperatures. Moisture was maintained by watering to weight. At harvest the plants were separated into tops and roots. In cases of doubt, the mycorrhizal nature of the short roots was determined by examination of sections stained with cotton blue in lactophenol. For analysis the tissue was dried at 70° C and ashed with $MgNO_3$ at 550–600° C. Phosphorus was determined by the molybdivanadophosphoric acid method (4). Following harvest, soil nitrate and ammonia, and phosphorus soluble in Morgan's extracting solution were determined (11).

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[3] Figures in parentheses refer to "Literature Cited", p. 345.

[4] R. O. ROSENDAHL. Mycorrhizae of forest trees: Their nutritional, ecological and silvicultural importance. Unpbl. Ph. D. thesis, University of Wisconsin, Madison. 1943.

EXPERIMENT 1

Portions of Panther Creek bentonite were saturated with various cations, then mixed with 18-mesh quartz sand and 0.2% magnetite. The calculated exchange capacity of the mixture was 7.4 m.e./100 grams with a saturation of 50% H, 40% Ca, 5% K, and 5% Mg. The pH was 4.70 which, at 50% base saturation, equaled the pK of the clay and was at or near the zone of minimum solubility of the phosphatic minerals added (14). The latter were purchased from Ward's Natural Science Establishment and ground to pass a 60-mesh sieve before mixing with the synthetic soil. Their composition and the quantities added per pot were:

Apatite	$Ca_5(PO_4)_3F$	2.0	gms
Dufrenite	$FePO_4 \cdot Fe(OH)_3$	3.0	"
Wavellite	$Al_3(OH)_3(PO_4)_2 \cdot 5H_2O$	2.0	"
Variscite	$AlPO_4 \cdot 2\,H_2O$	3.0	"
Monocalcium phosphate	(Reagent)	0.26	"

Sixteen pots of each soil-mineral mixture were sown in mid-September with two seeds per pot. Nitrogen and sulphur were supplied by later additions. In mid-April application of Hoagland's A–Z solution was required to relieve deficiency symptoms. From December to March the seedlings were illuminated 18 hours per day with an intensity of approximately 1,000 foot-candles. In February *Boletus luteus* was introduced. Half of the inoculated and of the uninoculated pots received weekly applications of 0.05 grams dextrose/pot from April to August. The seedlings were harvested 11 months after sowing.

EXPERIMENT 2

Pot cultures of the Carrington and O'Neill soils were established with factorial treatments of mycorrhizal inoculation and phosphate fertilization. Monocalcium phosphate at the rate of 425 lbs. P_2O_5/2,000,000 lbs. of soil was applied as a layer at midlevel. The pots were sown in December with two germinating seeds per pot and harvested the following October. Inoculation was delayed until April when light intensities were high (1). Repeated additions of *Boletus luteus* failed to inoculate the unfertilized cultures. Two months before harvest small quantities of soil from fortuitously inoculated replicates were introduced and, in the O'Neill cultures, resulted in the early stages of mycorrhizal infection.

Failure to obtain mycorrhizal inoculation where planned, as well as fortuitous inoculation elsewhere, destroyed the original design. Hence, seedling weights were grouped according to phosphate treatment and occurrence of mycorrhizae as observed at harvest. Fortuitous inoculation in the unfertilized cultures was indicated by the sudden return of normal green color and the initiation of height growth, the response appearing similar to that described by others (2, 3, 7, 9). The date when such changes became evident was noted and the presence of mycorrhizae later confirmed by inspection.

EXPERIMENT 3

It was thought that the possible effects of fungal activity upon the release of phosphorus to the soil solution might be detected by the growth of a companion crop. Accordingly Sudan grass, because of its extensive root system and sensitivity to phosphorus, was sown into mycorrhizal and nonmycorrhizal cultures of Monterey pine. The two soils were diluted 1–1 by weight with quartz sand and 200 grams of the Carrington sand or 225 grams of the O'Neill-sand mixture placed in each vessel. The green weights of pine seedlings transferred from nutrient solution were 2.3–2.9 grams for those planted in the Carrington soil and 2.0–2.1 for those planted in the O'Neill soil. Additional seedlings were used to determine the average green weight/dry weight ratio. The oven dry seedlings contained 0.25% P.

On June 1 each vessel was planted with one seedling. A 10-cm length of mycorrhizal white pine root was placed among the roots of each inoculated seedling and a similar length of autoclaved root with the noninoculated. Mycorrhizae were visible on the inoculated plants within a month. Germinated seeds of Sudan grass were sown on June 28 and later the plants were thinned to one per vessel except where growth was slight. All cultures were fertilized with potassium nitrate. All plants were harvested October 20.

RESULTS

EXPERIMENT 1

No differences in appearance other than between mineral treatments were observed. The occurrence of mycorrhizae at harvest bore no relation to inoculation and was apparently at random within a given phosphorus treatment; hence their presence is attributed to fortuitous inoculation. Each combination of variables, other than minerals, was constituted a treatment and an analysis of variance carried out (Table 1). The uniformity revealed

TABLE 1.—*Preliminary analysis of variance. Experiment 1.*

Source of variance	Degrees of freedom	Mean square	F
Total	94		
Minerals	5	27.86	188.1**
Treatments	7	.2236	N.S.
Interaction	35	.1481	N.S.†
Remainder	47	.1968	

** Significant at the 1% level.
† N. S. Not significant.

permitted disregarding all treatments except minerals and, within each of these, seedling weights were grouped according to the actual presence of mycorrhizae. Table 2 presents the mean dry weights with the exception of the calcium phosphate series which was entirely mycorrhizal. This table rests on the assumption that the mycorrhizae observed had been present long enough for any effect on phosphorus uptake to have been reflected in growth. None of the differences approach significance and hence under the conditions of this experiment mycorrhizae were without effect on phosphorus uptake from difficultly available minerals.

EXPERIMENT 2

Mean dry weights and tissue phosphorus contents are presented in Table 3.

It is clear that nonmycorrhizal seedlings grown on unfertilized soils contained very low levels of phosphorus in their tissues. After some initial growth such seedlings took on a characteristic stunted appearance that closely resembled that of seedlings in the minus-phosphorus cultures of Experiment 1. Stem elongation slowed and finally ceased with the uppermost needles becoming progressively shorter and more crowded, giving a tufted appearance to the seedling. All needles except the uppermost became a somewhat yellow- or tawny-green in color. Later progressive death of the oldest remaining needles occurred, and the stem elongated very slowly, producing short, crowded needles. At harvest such seedlings from the Carrington soil were found to contain

0.365 ± 0.034 mgm phosphorus per plant and those from the O'Neill cultures 0.028 ± 0.008 mgm P, as compared with seed contents of 0.220 mgm. and 0.234 mgm, respectively. Thus all of the phosphorus in 10½-month old seedlings grown in the O'Neill soil and nearly two-thirds of that in seedlings from the Carrington soil could be attributed to the initial seed supply. The formation of mycorrhizae, however, was followed by increased phosphorus content and resumption of normal growth.

On the Carrington soil phosphate fertilization by itself permitted normal seedling growth and phosphorus content and, under these circumstances, mycorrhizal infection was without additional effect. Comparison of the earliest inoculated seedlings on unfertilized soil with the seedlings from cultures receiving 425 lbs. P_2O_5 per acre suggests that mycorrhizal infection might be wholly equivalent in effect to phosphate fertilization if both were to act over the same period of time. Unfortunately, all seedlings in the O'Neill cultures with added phosphate had become mycorrhizal by the time of harvest so similar comparison cannot be made.

The data from seedlings fortuitously inoculated at successive times provide a picture of the progressive effects of mycorrhizal infection. Neither dry weight nor phosphorus content were immediately altered as the first short roots became mycorrhizal (Line 9, Table 3). As the mycorrhizal infection developed the seedlings accumulated phosphorus with but slight change in dry weight (Lines 2 and 10). The visible changes observed, *i.e.,* return of normal green color and initiation of height growth, are presumed to have been correlated with the

TABLE 2.—*Dry weights of mycorrhizal and nonmycorrhizal seedlings supplied with various phosphate sources. Experiment 1.*

	Dry weight (gms) of tops per pot				
	Check	Apatite	Variscite	Wavellite	Dufrenite
Nonmycorrhizal	(13)* 1.11 ± .05†	(3) 4.01 ± .03	(12) 2.23 ± .11	(10) 2.27 ± .15	(14) 2.06 ± .14
Mycorrhizal	(3) 1.30 ± .10	(13) 4.21 ± .11	(4) 2.16 ± .12	(6) 2.49 ± .22	(2) 2.43 ± .38

* Number of items composing mean.
† Standard error of mean.

TABLE 3.—*Dry weight and phosphorus content of pine seedlings in prairie soils. Experiment 2.*

Phosphate fertilization	Occurrence of mycorrhizae	No. of seedlings	Phosphorus content of needles	Dry weight of seedlings	Phosphorus contents of seedlings	Soluble soil phosphorus†
lbs. P_2O_5/A			%	gms	mgms	lbs./acre
			Carrington Silt Loam			
1 none	Non-myc.	10	0.048 ± 0.003‡	1.44 ± 0.07	0.729 ± 0.067	2.
2 none	Myc. 3–3½ mo.§	4	0.114 ± 0.010	1.45 ± 0.20	1.50 ± 0.39	1.
3 none	Myc. 4½–5 mo.	4	0.107 ± 0.010	4.86 ± 0.08	4.54 ± 0.93	1.5
4 none	Myc. 6 mo.	2	0.063 ± 0	8.88	6.10	1.
5 425	Non-myc.	6	0.095 ± 0.004	10.82 ± 0.44	10.49 ± 0.73	9.
6 425	Myc.	6	0.096 ± 0.005	11.11 ± 0.42	10.28 ± 0.55	10.
7 425	Myc., with soil mycelium¶	2	0.151 ± 0.016	12.17	18.14	8.
			O'Neill Sandy Loam			
8 none	Non-myc.	6	0.045 ± 0.005	1.01 ± 0.02	0.461 ± 0.042	1.
9 none	Incipient myc.‖	6	0.042 ± 0.005	1.11 ± 0.05	0.477 ± 0.035	1.
10 none	Myc. 1½ mo.	2	0.056 ± 0.003	1.09	0.662	1.
11 none	Myc. 3½ mo.	2	0.074 ± 0.007	2.72	2.0	1.
12 425	Myc.	8	0.132 ± 0.013	4.19 ± 0.18	5.29 ± 0.10	8.
13 425	Myc., with soil mycelium	8	0.184 ± 0.019	4.32 ± 0.23	6.95 ± 0.29	9.
	Difference (13–12)		+0.052 ± 0.023†† t = 2.26*		+1.66 ± 0.31 t = 5.41**	

* Significant at the 5% level.
** Significant at the 1% level.
† In Morgan's extractant, according to Peech and English (11). Values are means of variable number of tests.
‡ Standard error of the mean.
§ Time before harvest that first color changes in seedling following fortuitous inoculation were observed.
¶ "Soil mycelium" indicates dense growth of mycorrhizal fungus mycelium throughout soil at harvest.
‖ Inoculated with mycorrhizal soil 2 months before harvest. Plants with > 1 but < 25 mycorrhizal short roots, forked or simple.
†† Standard error of the difference.

TABLE 4.—*Comparative dry weights and phosphorus contents of Sudan grass and pine grown together as related to presence of mycorrhizae. Experiment 3.*

Treatment	No. replicates	Sudan grass		Monterey pine		
		Total dry weight	Total phosphorus content	Phosphorus content of needles	Gain in total dry weight*	Gain in phosphorus content*
		gms	mgm	%	gms	mgm
Carrington Silt Loam						
Nonmycorrhizal	5	2.81 ±0.15†	1.73 ±0.06	0.040 ±0.001	1.99 ±0.25	0.06 ±0.11
Mycorrhizal	5	0.112 ±0.018	0.066	0.080 ±0.008	3.71 ±0.10	2.33 ±0.07
O'Neill Sandy Loam						
Nonmycorrhizal	2	1.14, 1.07	0.64, 0.75	0.044, 0.047	1.51, 1.03	—0.07, 0.12
Mycorrhizal	2	0.26, 0.56	0.16, 0.30	0.059, 0.061	1.78, 1.50	0.44, 0.29

* Gains calculated from initial green weights of seedling, mean green weight/dry weight ratio, and mean percent P in seedlings at start of experiment.
† Standard error of mean.

great increase in phosphorus. Initially, at least, the high percentage content of phosphorus in the various tissues was maintained as their dry weight increased.

The seedlings in the stage of phosphorus accumulation prior to increase in dry matter were generally found to have only a fraction of the root system mycorrhizal; some had only a single strong lateral root affected. Except for the affected portions bearing numerous young mycorrhizae, forked and simple, the root systems were similar to those of nonmycorrhizal seedlings in unfertilized soil in appearance and extent.

The data of line 4, Table 3, and observations elsewhere indicate that the favorable phosphate status may not continue. These seedlings passed though the typical stages of needle color improvement and height growth early in the summer and attained appreciable size. By harvest the needles had lost color and the plants were growing only slowly; moreover, the percentage content of phosphorus now approximated that of the stunted nonmycorrhizal seedlings. Examination of the roots showed many suberized mycorrhizal structures but none with the succulent white tips characteristic of active mycorrhizae. This apparent decline of the mycorrhizal condition and seedling growth is very similar to an instance reported by Hatch (2).

A related phenomenon is evident from comparison of the seedling data of line 6 with 7 and 12 with 13, from the both fertilized and mycorrhizal Carrington and O'Neill soils, respectively. Although members of each pair were replicates and had the same greenhouse care, at harvest the soil in certain pots was found to be thoroughly penetrated with a network of mycelial strands connected to numerous young mycorrhizal tips. In the O'Neill cultures improved needle color and height growth were associated with the presence of this soil mycelium and the phosphorus contents of seedlings in both soils increased. Enough of the O'Neill cultures were affected to allow a "t" test of the significance of the differences (Table 3). The lack of dry weight differences and the appearance of needle color changes only shortly before harvest suggest that the mycelial development was recent. The causes leading to its differential appearance in replicate cultures are unknown.

TABLE 5.—*Dry weight of second sowing of Sudan grass in Carrington silt loam-sand mixture after harvest of pine. Experiment 3.*

Previous treatment	Dry weight of tops per tumbler (4 plants)	
	Phosphate added	Untreated
	gms	gms
Nonmycorrhizal	0.52, 0.38	0.21, 0.15
Mycorrhizal	0.55, 0.47	0.09, 0.09

Neither the initial occurrence of mycorrhizae nor the abundant development of mycelium influenced the sodium acetate- (Morgan's extractant) soluble phosphorus of the soil (Table 3). Available soil nitrogen was likewise unaffected; the unfertilized nonmycorrhizal, and the most recently infected cultures of Carrington soil contained 250–300 lbs. of nitrate-N/Acre, compared with 5–10 lbs./Acre in all cultures with larger plants. Respective values for the O'Neill cultures were 15–25 lbs. and 5 lbs. nitrate-N/Acre. There were no consistent differences in ammonia content.

EXPERIMENT 3

The dry weights and phosphorus contents of both pine and grass are presented in Table 4. Upon harvest the soil from each of four replicates of both treatments of the Carrington soil was air-dried and assigned to one of two subsequent treatments. The yield of Sudan grass from each of these is shown in Table 5.

The effects of mycorrhizae on the growth and phosphorus accumulation of the pine were similar to those reported in Table 3. Nonmycorrhizal seedlings in both soils failed to absorb any significant amount of phosphorus whatsoever; dry matter increase took place at the expense of the initial internal phosphorus supply.

The root of pine and grass intermingled freely in all cultures with no visible evidence of antagonism or decay. Purpling and death of the lower leaves characterized the Sudan grass in all cultures. There was no evi-

dence of benefit to the associated grass through release of phosphorus by the fungal mycelium. On the contrary, there was a reciprocal relationship between the growth of the pine and grass with the latter strongly suppressed in the presence of mycorrhizae. Such an effect, of course, could have resulted from pathogenicity of the mycorrhizal fungus but microscopic examination of the grass roots did not indicate this. Fungal invasion of grass roots was common but not extensive in both mycorrhizal and nonmycorrhizal cultures. As shown in Table 5, the repressive effect of the mycorrhizal soil on a second crop of Sudan grass, following removal of the pine seedling, was entirely overcome by phosphate addition. Moreover, the effect was less pronounced on the less fertile O'Neill soil where seedling weight increases were smaller and other observations, not reported here, indicate less effect in cultures with larger soil volumes. None of these observations suggest the action of a pathogenic fungus.

DISCUSSION

The outstanding consequence of mycorrhizal infection was the uptake by seedlings of soil phosphorus previously largely unobtainable (Tables 3 and 4). Nonmycorrhizal root systems in contact for months with soils containing low amounts of "available" phosphorus, as chemically determined, absorbed little or none of the native soil phosphorus although a portion of this was readily absorbed by Sudan grass or mycorrhizal pines.

The extent to which the mycorrhizal response can be explained in terms of phosphorus nutrition alone is not clear. The data of others (2, 8, 10) also indicates very low percentage contents of phosphorus in nonmycorrhizal seedlings and likewise the absolute contents are of the same order of magnitude as the estimated seed supply (9). The increased absorption of other nutrients by mycorrhizal pines reported by Hatch (2) and Mitchell, Finn, and Rosendahl (10) is not impressive when these are expressed as percentages, particularly in view of the acute phosphorus deficiency exhibited by the nonmycorrhizal seedlings. Moreover, such increases were not observed by McComb (7) in studies with the O'Neill soil. The results of Rosendahl[5] (12), demonstrating increased uptake of potassium from feldspar by presumably mycorrhizal seedlings in sand cultures, are difficult to explain other than by increased solubility of the mineral in the presence of the fungus. The increased potassium content and growth of the same seedlings after transfer to the Carrington soil, however, seem almost certainly confounded with phosphorus nutrition, in view of the evidence in Tables 3 and 4. Some workers (6, 7, 15) have postulated a mycorrhizal stimulus apart from any response due to improved mineral nutrition, and McComb and Griffith (8) have presented some evidence to that effect. In the present study no indication of such stimulus appeared. At the Licking Nursery in Missouri mycorrhizal inoculation and phosphate fertilization have brought about similar growth responses in pine seedlings (12, footnote).

The mechanism by which mycorrhizae render soil phosphorus available to the plant is likewise uncertain. In Experiment 1 no effect of mycorrhizae on the uptake of phosphorus from difficultly soluble minerals such as exist in the soil was observed. Although Routien and Dawson (13) believed the effect of mycorrhizae to be greater as the per cent base saturation of the substrate decreased, the saturation of the clay in Experiment 1 was less than the lowest involved in their studies. The evidence for a mechanism based upon a much greater absorbing surface presented by mycorrhizal roots, as proposed by Hatch (3), does not seem valid; apart from differences in the size of mycorrhizal and nonmycorrhizal seedlings, to compare the root system of a normal expanding plant with that of one in the advanced stages of phosphorus deficiency may badly confound cause and effect. The measurements of Routien and Dawson (13) have been taken to indicate that mycorrhizal roots have a much greater respiration than nonmycorrhizal roots. These comparisons, however, were based on equal lengths of long roots bearing nonmycorrhizal and hypertrophied mycorrhizal short roots, respectively, rather than on equal tissue masses.

Quantitative differences in absorbing area or metabolic activity of mycorrhizal and nonmycorrhizal root systems may possibly explain some differences in the relative uptake of phosphorus but do not account for the total lack of such uptake by nonmycorrhizal seedlings (Table 4). That this is not due to inability to absorb phosphate ions was indicated by the growth of nonmycorrhizal seedlings on phosphate fertilized Carrington soil. Likewise, with radio-phosphorus Kramer and Wilbur (5) demonstrated that although mycorrhizal roots absorb larger quantities of inorganic phosphorus from solution, nonmycorrhizal short roots absorb appreciable amounts. Further, the observations in Experiment 2 revealed that a large increase in the phosphorus content of a seedling occurred when only a fraction of its root system had become mycorrhizal, so that the phosphorus uptake was entirely out of proportion to the increased absorbing area of the plant *per se*.

The results of Experiment 3 suggest that fungal activity in the soil does not render phosphorus available to juxtaposed roots of other species. None of the evidence presented is inconsistent with a hypothesis of phosphorus transfer from fungus to root (1, 3, 6).

SUMMARY

Pot culture studies with Monterey pine grown in a synthetic soil containing ground phosphatic minerals failed to demonstrate any effect of mycorrhizae on phosphorus uptake by the seedlings. Similar cultures of pine in O'Neill sandy loam and Carrington silt loam showed that mycorrhizal infection was followed by accumulation of phosphorus by the plant and resumption of normal growth. Nonmycorrhizal seedlings failed to accumulate any considerable quantity of phosphorus from untreated soils but, on the Carrington soil, grew satisfactorily when phosphate fertilizers were supplied. It is concluded that at least much of the mycorrhizal response in pine can be attributed to improved phosphorus nutrition.

[5] Loc. cit.

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